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# Journal of Animal Ecology

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## **Micro- and macroparasite species richness in birds: the role of host life history and ecology**

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## Abstract

1. Identifying the factors shaping variation in parasite diversity among host species is crucial to understand wildlife diseases. Although micro- and macroparasites may exert different selective pressures on their hosts, studies investigating the determinants of parasite species richness in animals have rarely considered this divide.

2. Here, we investigated the role of host life history and ecology in explaining the species richness of helminths (macroparasites) and haemosporidians (microparasites) in birds worldwide. We collated data from multiple global datasets on diverse bird traits (longevity, body mass, coloniality, migration distance/tendency, geographic range size and dietary and habitat breadths) and the species richness of their helminth and haemosporidian parasites. We tested predictors of helminth and haemosporidian parasite richness using phylogenetic generalised linear mixed models in a Bayesian framework.

3. We found that, after controlling for research effort and host phylogeny, the richness of helminths, but not of haemosporidians, increased with host longevity, range size, migration distance and dietary breadth. Overall, these correlates were also important across different helminth groups (acanthocephalans, cestodes, nematodes and trematodes), and two additional ones (body mass, coloniality) emerged as important for cestodes and acanthocephalans.

4. We propose that long lifespans may promote the diversity of helminth parasite assemblages over evolutionary time, thus resulting in richer helminth faunas. Similarly, longer-distance migrations, larger ranges and broader dietary breadths are likely to lead to greater encounter rates and the accumulation of trophically-transmitted helminths. In contrast, vector-borne haemosporidians may be influenced more by factors related to vector ecology than by the host traits included in the analyses. The lack of strong associations

between haemosporidian species richness and host characteristics emphasizes the need to find appropriate traits to model the distribution and diversity of parasites with different environmental preferences in order to anticipate disease emergence risks associated with global change.

**Key words:** birds, comparative method, haemosporidians, helminths, host-parasite interactions, life history, parasite diversity

## Introduction

Identifying the factors shaping variation in parasite diversity among host species is crucial to understand diseases of human and wildlife populations, including their infection risks and host investments into defences (Stephens et al., 2016). Although certain parasite species have profound effects on host fitness and can cause rapid population declines, or even extinctions, in both plants and animals (De Castro & Bolker, 2005; Fisher et al., 2012), single infections are rare in nature. Rather, infections with multiple parasite species are the norm in natural systems at individual, population and species levels (Bordes & Morand, 2011).

Notably, parasite diversity has been reported to be associated with the genetic diversity of the major histocompatibility complex, levels of immune investment and the susceptibility to other parasites, reduced survival and fecundity, and the evolutionary diversification of host species (Bordes & Morand, 2015). At the same time, examining parasite biodiversity is an important aspect of ecology because parasites make up a large percentage of overall biodiversity and can influence ecosystem processes (Hudson, Dobson, & Lafferty, 2006).

Over the past four decades, a number of comparative studies have searched for correlates of parasite species richness at the host species level across major host groups (Arriero & Møller, 2008; Gregory, 1990; Leung & Koprivnikar, 2016; Lindenfors et al., 2007;

Nunn, Altizer, Jones, & Sechrest, 2003). These investigations have found several associations between parasite species richness and host species traits and other ecological factors such as body size, geographic range size, host population density, and latitude (Bordes & Morand, 2015; Poulin & Morand, 2004). The direction and significance levels of these associations are often inconsistent, however (Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014; Morand, 2015). In a recent meta-analysis, Kamiya et al. (2014) showed that host body size, geographic range size and population density are positively correlated with parasite species richness across animal, plant and fungal hosts. However, their meta-analysis also revealed that in some cases the effect of these 'universal' predictors depends on either the hierarchical level of the data used for analysis or the spatial scale of the study. Moreover, the effects of other predictors of parasite species richness at the host species level proposed in the primary literature remain to be addressed across a range of taxonomic groups (see Table 1 for a list with several correlates of parasite species richness of vertebrates).

In addition, comparative studies considering combinations of major parasite groups such as macro- and microparasites are needed to understand the impacts and determinants of parasite species richness in natural systems (Bordes & Morand, 2009). Importantly, Lindenfors et al. (2007) showed that the determinants of parasite species richness in mammalian carnivores differ among different parasite groups with different transmission modes. Furthermore, a recent study examining global patterns of helminth parasite sharing between mammalian wildlife species and domestic mammal hosts showed that host sharing is more strongly linked to the diet strategy of the host species rather than the environmental conditions (Wells et al., 2018). In contrast, transmission patterns in vector-borne haemosporidians are strongly influenced by environmental factors (Loiseau et al., 2012; Pérez-Rodríguez, Fernández-González, De la Hera, & Pérez-Tris, 2013). Unlike microparasites, the majority of parasitic helminth species do not replicate in the definitive vertebrate host, with many species requiring transmission through a diversity of intermediate

hosts to complete their life cycles. Thus, different mechanisms may apply in relation to how macro- and microparasites are spread through and maintained in host species.

The selective pressures exerted on hosts possibly also differ between micro- and macroparasites. Microparasites (viruses, bacteria, fungi and protozoa) are characterized by their relatively short duration of infection, and their tendency to produce a sustained immune response in infected vertebrate hosts (Hatcher & Dunn, 2011). In contrast, macroparasites (helminths and arthropods) produce infective stages that usually pass out of the host before transmission to another host; they tend to produce a limited immune response in infected hosts and are relatively long-lived (Hatcher & Dunn, 2011). It is thus likely that the two classes of parasites would lead to different selection pressures on hosts and differentially affect the evolution of life history traits, warranting further research efforts.

For instance, life-history theory predicts that the direct costs of parasite exploitation should cause a negative association between parasite species richness and host longevity at the species level (Arriero & Møller, 2008; Cooper, Kamilar, & Nunn, 2012; Ezenwa et al., 2006; Morand & Harvey, 2000). Life-history theory also predicts that host species with higher adult survival rates should invest heavily in immunity (Lochmiller & Deerenberg, 2000); indeed, this may explain a negative association between host survival rate and parasite species richness observed in pathogenic haemosporidian microparasites of birds (Arriero & Møller, 2008). In contrast, epidemiological theory suggests that there should be a positive association between host longevity and parasite species richness since longer-lived hosts are likely to be exposed to (and may accumulate) more parasites throughout their lifetimes, at both the individual (Piersma & van der Velde, 2012) and species levels (Lindenfors et al., 2007). Although these processes typically occur over ecological time scales by infection and demographic processes, they might lead to the gradual development of component communities (i.e. parasite communities within host populations) which ultimately shape parasite faunas at the host species level (Poulin & Morand, 2004). Such a pattern has been suggested in less pathogenic and virulent helminths (Poulin & Morand, 2004). Hence, life

history traits such as host longevity can be determinants of, as well as responses to, parasite species richness. The direction of the causality is likely to be dependent on the life history of parasites and the resulting selection pressures on their hosts may differ between major parasite groups such micro- and macroparasites.

Here we present the first global-scale analysis of the correlates of helminth (macroparasite) and haemosporidian (microparasite) species richness in birds. To do so, we collated data from multiple global datasets on diverse bird traits (longevity, body mass, coloniality, migration distance, geographical range size, dietary and habitat breadths) and the species richness of their helminth and haemosporidian parasites. Helminths are parasitic worms belonging to the phyla Platyhelminthes (trematodes and cestodes), Nematoda (nematodes) and Acanthocephala (acanthocephalans); the majority of helminths are trophically transmitted to their definitive hosts via infected prey before reproducing in high-trophic-level hosts, such as birds, in which they invade a variety of organs and tissues (Atkinson, Thomas, & Hunter, 2008). On the other hand, avian haemosporidians (phylum Apicomplexa: order Haemosporida: *Plasmodium*, *Haemoproteus* and *Leucocytozoon*) are blood-borne parasites transmitted between their vertebrate hosts by blood-feeding dipteran insects (Valkiūnas, 2005). Besides their different transmission modes, these macro- and microparasites also have different pathogenic effects, with helminths frequently being less pathogenic and virulent than haemosporidians (John, 1995), although pathogenicity can vary within groups (Atkinson et al., 2008; Valkiūnas, 2005). Given the different transmission modes and levels of pathogenicity of helminths and haemosporidians, we predict differential importance of the associations between the richness of these two major groups of bird parasites and the life-history and other ecological traits of their hosts (see Table 1 for hypotheses and predictions). With our analyses, we identified strong correlates of helminth but not haemosporidian species richness.

## 2 | METHODS

### 2. 1 | Parasite species richness

Parasite assemblages can be studied at various hierarchical levels, from *infracommunity* (all parasite species at the level of individual hosts), to *component community* (all parasite species at the level of host populations) or *parasite fauna* (all parasite species at the level of host species, either regionally or globally) (Poulin, 2007). Comparative studies on the evolution and ecology of parasite species richness have typically focused on the two latter assemblages, and the epidemiological and ecological processes considered to generate them are the same (Poulin, 2007; Poulin & Morand, 2004). Theoretically, the maximum number of species in a component community is set by the size of the parasite fauna; in fact, empirically the maximum or average richness of component communities typically increases with the richness of the parasite fauna among host species — at least until a certain point where component communities might become saturated with species (Kennedy & Guégan, 1994). It is therefore not surprising that some comparative studies of helminth end parasite communities across vertebrate hosts found almost identical results when using parasite species richness across host populations or across host species (Poulin & Leung, 2011). For this reason, in order to examine the potential reasons why certain host species have evolved richer faunas than others, it makes sense to correlate ecological variables with the richness of component communities and parasite faunas across host species (Poulin & Morand, 2004).

Here we considered parasite species richness as the total number of helminth or haemosporidian species recorded per host species, i.e. the observed (rather than true) richness of helminth and haemosporidian faunas. We focused on these two parasite groups because (i) they are commonly found in wild bird populations and can wield important selection pressures on their hosts through effects on survival (Hudson, Dobson, & Newborn, 1992; Marzal, Bensch, Reviriego, Balbontin, & De Lope, 2008; Møller & Nielsen, 2007),



reproductive success (Amundson & Arnold, 2010; Hudson, 1986; Marzal, de Lope, Navarro, & Møller, 2005; Merino, Moreno, Sanz, & Arriero, 2000), or the expression of nuptial plumages (Hörak, Ots, Vellau, Spottiswoode, & Møller, 2001; Piersma et al., 2001); and (ii) they are well-studied taxonomic groups, providing good data availability (see below). We used the dataset in (Healy et al., 2014) as starting point to build a global dataset on parasite richness in bird hosts. This dataset includes data on several ecological and life history traits of birds and mammals, including high-quality data on maximum longevity—a life-history parameter expected to covary with parasite species richness (see *Introduction*). We used the bird species data from this database ( $n=589$ ) and then used two databases to collect helminth and haemosporidian richness for these species (Appendix S1 in Supporting Information).

We searched for helminth records (acanthocephalans, cestodes, nematodes and trematodes) for each bird species in the subset by using the global database of host–helminth parasite occurrence records maintained by the London Natural History Museum (NHM) (Gibson, Bray, & Harris, 2005). This curate database includes more than 250,000 global host–helminth records from over 28,000 published peer-reviewed articles added since 1922. As the current version of the NHM database only reflects records added to the end of 2003, this was supplemented by a Web of Science search, up to the end of 2015, for each bird species (Appendix S2). We counted the number of parasite species listed for each bird species after considering taxonomic issues (e.g. ‘double-counting’ parasite species with revised classification; Appendix S2) by querying the database through the package ‘HelminthR’ (Dallas, 2016). For some host-parasite records, parasites were identified to the genus-level only. To use as much data as possible, we include these parasites in estimates of parasite species richness provided that no other members of the genus were recorded for the host species (Cooper et al., 2012).

Additionally, we extracted haemosporidian richness from the MalAvi database (Bensch, Hellgren, & Pérez-Tris, 2009). This database contains avian malaria parasites (*Plasmodium* spp.) and related haemosporidians (*Haemoproteus* and *Leucocytozoon* spp.). In this database, unique haemosporidian lineages are identified based on sequence data from a fragment of the cytochrome-*b* gene that is commonly targeted in molecular studies of avian haemosporidians, reducing the risk of using multiple names for identical lineages. This database includes host–haemosporidian records from published peer-reviewed articles since 2000, the year when the first general protocol for amplification of cytochrome *b* sequences was published (Bensch et al., 2000). Again, we collected data up to the end of 2015. This generated a single value for each bird host species from this database with respect to number of unique parasite species in each host.

For each host species, we calculated total helminth and haemosporidian species richness as well as species richness for the different helminth groups (acanthocephalans, cestodes, nematodes and trematodes). Parasite species richness data are sensitive to sampling effort (Walther, Cotgreave, Price, Gregory, & Clayton, 1995). To control for sampling bias, we included a measure of sampling effort for each host species (following similar approaches used by e.g. Nunn et al., 2003; Ezenwa et al., 2006; Lindenfors et al., 2007; Cooper et al., 2012). We defined this as the number of *Web of Science* references (citation count, see Appendix S3). We derived citations counts for each host species and search string, i.e. helminth and haemosporidian counts. As we were interested in patterns of natural infections in wild hosts, studies using experimentally infected or captive birds were excluded. We assembled a comprehensive dataset on helminth/haemosporidian species richness and various ecological/life-history traits of 349 host species (Gutiérrez, Piersma, & Thieltges 2019). Our dataset included species with land and marine distributions, spanning virtually every habitat type but Antarctic land masses (Fig. 1).

## 2.2 | Host ecology and life history traits

We collected data on host ecological and life history traits that can potentially influence parasite species richness at the host species level in vertebrate hosts (see Table 1 for hypotheses and predictions):

*Body mass and longevity.* We used the data on birds' maximum longevity (years) and body mass (g) as reported in (Healy et al., 2014). The authors excluded species with maximum longevity estimates based on fewer than 10 longevity records, or with low or questionable data quality as defined in the AnAge database (de Magalhães & Costa, 2009). As maximum values are dependent on sample size, they also ran a sensitivity analysis excluding species with maximum longevity estimated from fewer than 100 longevity records and demonstrated that their analysis was robust and their conclusions were unaffected by sample size (Healy et al., 2014).

*Colonial breeding.* We also classified bird species as colonial, non-colonial, or semicolonial using information from the *Handbook of the Birds of the World Alive* (del Hoyo, Elliott, Sargatal, Christie, & de Juana, 2015). These categories are described in detail in Appendix S4.

*Geographic range size and migratory activity.* We used species-level geographic range maps from BirdLife International to extract species' geographic range. To do this, we converted species' ranges into a presence-absence matrix (1° grid cell) and then summed the number of cells (area in km<sup>2</sup>) in which each species occur using the package 'letsR' (Vilela & Villalobos, 2015). Here we focused on the parasite fauna of host species across their entire range, so we included range polygons regardless of their seasonality ('resident', 'breeding season', 'non-breeding season', and 'passage'; Fig. 1). We also estimated species' migration distances as the distance (km) between their breeding and nonbreeding range centroids (Gutiérrez, Rakhimberdiev, Piersma, & Thieltges, 2017). We acknowledge that differences among populations of a given species occur with respect to the presence or

absence of migratory activity and in the amount or type of activity (e.g. total distance covered). To account for within-species variation in migratory behaviour we additionally sorted species into three broad categories along an ordinal scale: (1) resident over whole global range, (2) population partly resident, partly migratory, and (3) fully migratory (Gutiérrez et al., 2017).

*Dietary and habitat breadths.* We used the EltonTrait database (Wilman et al., 2014) to collect dietary data. This database describes semi-quantitative dietary information for all extant bird species. For each species, diet is described using ranked percentages (in 10% increments) reflecting the estimated relative usage of 10 food categories. We analysed the ranked percentages as a continuous trait and also reclassified them into binary format: absent (percentage=0) or present (percentage>0) (Olalla-Tárraga, González-Suárez, Bernardo-Madrid, Revilla, & Villalobos, 2016). Dietary diversity was computed as: (1) dietary breadth: total number of dietary categories consumed, based on presence/absence data; and (2) the standardized Levin's index of dietary diversity: calculated as  $B_A = \frac{B-1}{n-1}$ , where  $n$  is the number of possible food of each food categories and  $B = \frac{1}{\sum p_j^2}$ , where  $p_j$  was calculated using ranked proportions (Olalla-Tárraga et al., 2016). We downloaded species' habitat information from IUCN RedList (<https://www.iucnredlist.org>, accessed in June 2016) using the package 'letsR' (Vilela & Villalobos, 2015). This generated a dataset with species names and the habitats where they occur ('1' if species is present and '0' otherwise). The 'Habitats Classification Scheme' from IUCN RedList describes the major habitat classes in which taxa occur and take into account biogeography, latitudinal zonation and depth in marine systems. Of the main 17 habitat classes listed in this scheme, two classes ("Marine Deep Ocean Floor" and "Introduced Vegetation") where bird species do not occur were deleted, resulting in 15 potential habitat classes. For each species, we calculated habitat breadth as the number of occupied habitat classes (range=1-10, median=4). We further calculated the species habitat specialization index from the number of occupied habitat classes (Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006). Assuming equal densities in occupied habitat and

null density in others, habitat specialization index for a species present in  $h$  habitat classes among  $H$  possible habitat classes is

$$\text{habitat specialization index} = \left( \frac{h}{H} - 1 \right)^{1/2}$$

Among our species, habitat specialization index ranged from 0.71 (equivalent to present in  $\approx 10$  of 15 habitat classes) for the generalist peregrine falcon (*Falco peregrinus*) to 3.74 (equivalent to present in  $\approx 1$  of 15 habitat classes) for the American bittern (*Botaurus lentiginosus*) or the western capercaillie (*Tetrao urogallus*) as habitat specialists.

We are aware of the potential influence of other variables (e.g. latitude and landmass type) on the biogeography of host-parasite interactions and, ultimately, the parasite species richness of hosts (Morand, Bordes, Pisanu, Goüy Joëlle, & Krasnov, 2010). However, a recent meta-analysis (Kamiya et al., 2014) showed that the latitude at which hosts live is not a universal predictor of parasite species richness across animal, plant and fungal hosts. Furthermore many (but not all) species in our dataset were fully or partly migratory, rendering latitude to be relatively meaningless in this case as it will be confounded by migration distance (distance between breeding and non-breeding range centroids, see above). Regarding the effects of landmass type (e.g. island versus mainland), there is some evidence that parasite species richness is poorer in insular than in continental host populations (Morand et al., 2010). At the host species level, however, landmass type is difficult to obtain because some bird species include island and mainland populations and others use different landmass types across different phases of their annual cycle. Therefore, we did not include these variables in our analyses.

### 2.3 | Phylogenetic trees

We used the bird phylogeny from the BirdTree project (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012), which encompasses all extant bird species (<http://birdtree.org>). A distribution

of 10,000 trees with different topologies was obtained for the 349 species for which we had helminth and/or haemosporidian data. To account for phylogenetic uncertainty, we randomly sampled 100 trees from this posterior distribution of trees (Appendix S5).

## 2.4 | Statistical analyses

We performed all statistical analyses in *R* version 3.3.1 (R Core Team, 2016). We fitted Bayesian phylogenetic mixed models using the package 'mulTree' (Guillerme & Healy, 2014), which performs 'MCMCglmm' models (Hadfield, 2010) on multiple phylogenetic trees. Parasite species richness was included as the response variable; longevity, body mass, migration distance, geographic range size, dietary/habitat breadths, and coloniality (colonial, non-colonial, semi-colonial) as predictors; and host phylogeny as random effect. Continuous raw predictors were centred and scaled to improve model performance and parameter estimation. Models of parasite species richness were analysed with a Poisson error distribution, which deals with any over-dispersion in the data after accounting for fixed and random sources of variation (Hadfield, 2010). To reduce collinearity between variables, we first checked that variables had Pearson's correlation coefficients  $<|0.7|$  (Dormann et al., 2013) (see Appendix S6). Then, we retained variables with variance inflation factors of less than three (Dormann et al., 2013).

We ran three sets of models (i.e. they were run on the 100 randomly sampled trees) using total helminth and haemosporidian richness. First, we ran separate sets of single-response models for total helminth and haemosporidian richness. Second, we performed the same type of analyses using a 'reduced dataset' containing only host species for which we collected data on both helminths and haemosporidians ( $n=124$ ; Appendix S7). Third, using the reduced dataset, we implemented a multi-response approach with total helminth richness and haemosporidian richness as response variables, and we tested for covariance between them (see Appendix S7 for more details). We used single- and multiple-response

models based on the reduced data set only to compare the results with the ones from the full data set in an effort to verify that our inferences were not affected by potential taxonomic or geographical sampling biases in the full dataset (i.e. some host species and regions are better studied than others). In addition, we used multi-response models based on the reduced data set only to investigate whether there was a statistically significant difference between the two parasite groups for a given predictor. As our analyses were in a Bayesian framework, here 'significant' is used as a synonym for important. Predictors were judged significant if the estimates of the 95% credible intervals (CI) did not cross zero. Significant interaction terms would indicate whether there is a statistical difference between the two parasite groups for a given predictor. While in single-response models different predictors may turn out to be significant in the separate models, this does not mean that the general directionality of these predictors differs between the two groups in a strict statistical sense.

In addition to the models using total helminth and haemosporidian richness, we also ran single-response models for the four major helminth groups (trematodes, cestodes, nematodes and acanthocephalans) to account for the larger taxonomic coverage within the helminths compared to the haemosporidians (Appendix S8).

To broadly explore ecological (geographic range size, habitat and dietary breadths) and life-history (mass, longevity) potential differences among resident, partly migratory and fully migratory bird species, we also ran separate models with each ecological and life history traits as response variables and migratory behaviour as the predictor variable using the full dataset. These models were analysed with a Gaussian error distribution (Appendix S8).

For all analyses, we used an uninformative prior (with variance set to 0.5 and belief parameter set to 0.002) for fixed effects and ran two chains for 5,000,000 iterations with a thinning value of 2,500 after a burn-in of 100,000. Potential scale reduction values were all less than 1.1 and the autocorrelations of posterior samples were all less than 0.1. Effective

sample sizes for all fixed effects were all greater than 1,000. We estimated the importance of host species' shared evolutionary history using heritability ( $h^2$ ), a measure of phylogenetic signal ranging between 0 and 1, that can be calculated from the estimated phylogenetic variance in the model (Hadfield, 2010). The interpretation of  $h^2$  is identical to that of Pagel's  $\lambda$  in phylogenetic generalised least squares models (Freckleton, Harvey, & Pagel, 2002), such that values close to 0 indicate that there is negligible effect of phylogeny, and values close to 1 that there is strong phylogenetic signal in the data. We calculated  $h^2$  across the entire posterior distribution.

## 2.5 | Methodological considerations

We note that there are several methodological issues that may have impacted our results, although we do not think that they compromise our main inferences. First, although we included data from several sources parasite richness and host trait data used in our study relate to the species level, which avoids comparisons at different scales (e.g. parasite richness at the host-population *versus* the species level). We are aware, however, that bird populations of a given species may exhibit differences in several traits (notably migration strategies), and taking a comparative approach at the species level may cause quantitative biases in our parameter estimates. In an effort to reduce the potential effects of within-species variation in migration strategies, we ran separate models in which species' migratory behaviour was classified into three broad categories (see above).

Second, the sample size for the two main parasite groups differed substantially (Figs. 1-3), potentially biasing parasite species richness comparisons. Therefore, we ran separate analyses for helminth and haemosporidian species richness using the reduced dataset. The results from the analyses using the reduced dataset did not change our conclusions (see below).



Third, taxonomic coverage for microparasites was significantly poorer than for macroparasites because of data limitations. Although the order Haemosporida is a large group of vector-borne protozoan parasites commonly found in vertebrates (Valkiūnas, 2005), we did not include other microparasites such as viruses, bacteria or fungi with other modes of transmission (direct, faecal-oral, or trophic transmission). Efforts to document known host–parasite associations in large databases are fairly recent (Bensch et al., 2009; Gibson et al., 2005; Nunn & Altizer, 2005; Stephens et al., 2017; Strona, Palomares, Bailly, Galli, & Lafferty, 2013) and global databases encompassing both micro- and macroparasites (including viruses, bacteria, protozoa, fungi, helminths and arthropods) are still restricted to mammals to date (Stephens et al., 2017). Future global datasets on several diverse taxa of avian (micro-)parasites will offer opportunities to expand on present work and make new discoveries.

Fourth, data quality in databases such as NHM (Gibson et al., 2005) and MalAvi (Bensch et al., 2009) is highly heterogeneous. The former includes helminth parasites morphologically identified by microscopy techniques, whereas the latter includes avian haemosporidian parasites identified by molecular analyses of DNA extracted from blood samples. Molecular techniques are better at detecting weak infections and cryptic species (Bensch et al., 2009). Thus, the limited morphological characters of some parasitic helminths might have resulted in an underestimation of the true number of parasite species in the NHM database. On the other hand, a full examination of the host's entire carcass and internal organs and the much longer sampling period of the NHM database may counteract the underestimate caused by using microscopy techniques. Nevertheless, it is important to remember that we ran separate analyses for helminth and haemosporidian richness, which partly account for the idiosyncrasy of these parasite-specific databases. Our results were conducted at a broad phylogenetic scale, and it is possible that more fine-scaled studies within different avian and parasite clades might find somewhat different patterns.

Finally, variation in pathogen and parasite assemblage structure can vary across zoogeographical regions (Olival et al., 2017; Wells et al., 2018). Geographical sampling bias (i.e. some host species and regions are better studied than others) may therefore complicate the detection of underlying patterns of species richness. To avoid sampling bias when making inferences about host–parasite associations, we also ran analyses using the reduced dataset.

### 3 | RESULTS

Helminth richness (mean=29, range=1-264) was dominated by trematodes, followed by cestodes, nematodes and acanthocephalans (Fig. 2). Haemosporidian richness (mean=6, range=1-47) was dominated by *Plasmodium*, followed by *Haemoproteus* and *Leucocytozoon* (Fig. 2).

As expected, citation counts (our measure of sampling effort) were positively correlated with total helminth and haemosporidian parasite richness (see Fig. 3 and Appendices S3 & S7). Maximum longevity, migration distance, geographic ranges size and diet breadth were positively correlated with total helminth parasite richness. Habitat generalists (species with low scores of habitat specialization) tended to harbour more helminth parasites (Fig. 3 and Appendix S7). In addition, our results show that partly migratory species were longer-lived than migratory and resident species, but there was no difference among the three groups with respect to body mass (Appendix S9). Overall, resident species had smaller geographic ranges, but broader dietary and habitat breadths, than partly/fully migratory species (Appendix S9). In stark contrast, haemosporidian richness was not correlated with any of the host traits analysed. When using the reduced dataset (only bird species with complete helminth and haemosporidian data), the effects of research effort and migration distance became negligible ( $\beta = 0.122$ , 95% CI= -0.040–0.294 and  $\beta = 0.202$ , 95% CI= -0.023–0.431, respectively), while dietary breadth became a stronger

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predictors of helminth richness ( $\beta = 0.317$ , 95% CI= 0.091–0.543) (Appendix S7).

Phylogenetic signal (measured as the mean  $h^2$  in our models) was low for the haemosporidian richness models ( $h^2=0.237$ ) and relatively high for the helminth richness models ( $h^2=0.639$ ) (Fig. 4 and Appendix S7).

Multi-response models, directly comparing patterns of total helminth and haemosporidian richness, yielded similar results, with the exception that habitat specialization became a marginally significant predictor of total helminth richness ( $\beta=-0.116$ , 95% CI=-0.239–0.008; Appendix S7). These models also show that there were no significant interactions between the two parasite types for the predictors examined (Appendix S7). Thus, there was no statistically significant evidence for a difference between the slopes of any predictor in helminth and haemosporidian richness (i.e. our two responses).

When considering the four major helminth groups separately in additional single-response models, we generally found similar predictors of parasite richness as in the analyses using total helminth richness. However, depending on the helminth group, some of predictors found at the total helminth level (maximum longevity, migration distance, geographic ranges size, diet breadth) were not maintained at the within-helminth level and others (body mass, coloniality) emerged. Trematode species richness was higher in longer-lived and smaller-bodied hosts with larger geographic ranges and longer migratory distance; it also tended to be higher in hosts species with broader dietary and habitat breadths (Fig. 5). Likewise, nematode species richness increased with host longevity and range size, but was not affected by the other predictors (Fig. 5). Similarly, cestode species richness correlated positively with host longevity, geographic range size, diet breath; moreover, cestode richness was lower in non-colonial host species than in colonial and semi-colonial ones. Finally, acanthocephalan species richness increased with migratory distance, but decreased with body mass; it also tended to increase with longevity (Fig. 5).

## 4 | DISCUSSION

We combined multiple, global-scale datasets on bird traits and their parasites to ascertain the main predictors of helminth and haemosporidian species richness. We found that, after controlling for research effort and host phylogeny, total helminth richness positively correlated with host longevity, geographic range size, dietary breadth and migration distance. The same predictors were found across the different helminth groups (acanthocephalans, cestodes, nematodes and trematodes), with some variation in their significance and additional predictors (body mass, coloniality) emerging. Surprisingly, however, haemosporidian species richness was not correlated with any of the host traits examined in this study.

Despite this unexpected contrast of finding several strong predictors for helminth richness and none with haemosporidians, our multi-response analyses did not reveal statistically significant interactions between predictors and the two parasite groups. Hence, while predictors in the single-response models obviously differed between the two parasite groups, our multi-response analyses do not support the hypothesis that there are statistically significant differences between the two groups in the role of host life history and ecology in determining parasite richness of birds. This may relate to the generally greater explanatory power of the respective variables for helminths than for haemosporidians. The latter group showed a smaller variation in species richness but wider credibility intervals (see Figs 2 & 3, respectively), suggesting that model estimates may be less precise for haemosporidians. Furthermore, multi-response procedures may have produced complex models with a tendency to overfitting which would have obscured differences between helminth and haemosporidian species richness.

Although from a statistical point of view it remains open whether there are actual differences between the two parasite groups in the role of host life history and ecology in determining parasite richness of birds, the presence of many significant correlates within

helminths but none in haemosporidians is intriguing and may be linked to ecological differences between the groups. It is possible that the richness of vector-borne haemosporidians may be influenced more by environmental factors related to vector ecology not captured as explanatory variables in our analysis (Loiseau et al., 2012; Pérez-Rodríguez et al., 2013). Indeed, climatic variables and landscape features are important predictors of local haemosporidian parasite richness in birds (Clark et al., 2018; Pérez-Rodríguez et al., 2013). Moreover, some haemosporidian vectors are also known to be habitat specialists; for example, *Haemoproteus* vectors rely on constant ground humidity, and *Leucocytozoon* vectors require running, unpolluted water for breeding (Santiago-Alarcon, Palinauskas, & Schaefer, 2012). There is also evidence that bird species inhabiting marine habitats have lower presence and richness of blood parasites than species inhabiting inland areas due to the scarcity of insect vectors in marine habitats (Clark, Clegg, & Klaassen, 2016; Mendes, Piersma, Lecoq, Spaans, & Ricklefs, 2005; Piersma, 1997), which does not hold for trophically-transmitted helminths (Gutiérrez et al., 2017). Finally, feeding patterns of vectors (including host compatibility) can influence the host range of avian malaria species (Medeiros et al. 2013), which may ultimately play a role in shaping the diversity of malaria infections in avian hosts. Therefore, environmental variables and vector ecology may better explain the richness of vector-borne parasites in avian species.

In regard to helminth infections, our analysis identified several significant determinants of overall and group-specific helminth richness in birds. The observed increase of overall helminth richness and group-specific richness (except for that of acanthocephalans) with host longevity is consistent with epidemiological theory and previous studies from mammals showing that longer-lived hosts are more likely to be exposed to more parasites throughout their lifetime (Poulin & Morand, 2004). It is thus possible that long lifespans promote the diversity of helminth parasite assemblages over evolutionary time, thus resulting in richer helminth faunas. However, a more recent comparative study in mammals using larger datasets and more advanced phylogenetic methods revealed no or a

weak (depending on host and parasite group) negative relationship between parasite species richness and host species longevity (Cooper et al., 2012). One possible explanation for our diverging results is that longer-lived birds—they live up to four times longer than similar-sized mammals (Healy et al., 2014)—might need to invest more in immune defences compared to mammals. Indeed, baseline immune investment increases with higher macroparasite parasite species richness in birds (John, 1995; Koprivnikar & Leung, 2015; Poulin & Morand, 2000) and mammals (Bordes & Morand, 2009; Cooper et al., 2012). Therefore, it is tempting to speculate that any potentially negative impact of parasite richness on host longevity as resulting from higher parasite richness in longer-lived birds is offset by effective immune defence strategies so that the positive relationship between longevity and helminth richness resulting from epidemiological processes remains visible.

As expected, helminth richness (except for that of acanthocephalans) increased with geographic range size, indicating that host species with a broad distributional range are more likely to encounter and be colonised by several parasite species over evolutionary time (Kamiya et al., 2014). Likewise, overall helminth richness and trematode and acanthocephalan richness increased with migration distance. This is line with previous studies showing that migratory birds often have greater parasite richness compared to non-migratory species (Figuerola & Green, 2000; Koprivnikar & Leung, 2015; Leung & Koprivnikar, 2016). This might be driven by the metabolic and physiological demands of migration, differential selection on host life-history traits or basic ecological differences between migratory and non-migratory species (Leung & Koprivnikar, 2016). Although we found some differences in the ecology and life history of resident and migratory species (migratory species had larger geographic ranges and narrower dietary/habitat breadths compared with resident species), they cannot fully explain the differences in helminth species richness between migratory and non-migratory species. While the larger geographic ranges of migratory species may facilitate the establishment of larger numbers of parasites, their higher levels of ecological specialization are expected to have an opposite effect. This

finding indicates that there might be other factors directly related to migratory habits driving this pattern (Leung & Koprivnikar, 2016), and suggests that the high energetic demands of long-distance migrations may cause increased susceptibility to parasitic helminths. Birds may exhibit reduced immunocompetence to assist in meeting the demands associated with the migratory period (Owen et al., 2006). Consequently, immunocompromised birds may be more susceptible to parasite infection at stopover sites (Owen et al., 2006).

On the other hand, long-distance migrations can lower parasite transmission by allowing hosts to escape parasites or by culling sick animals (Altizer, Bartel, & Han, 2011; Piersma, 1997). It is important to remember that although such processes often occur over ecological time scales by infection and demographic processes at the infracommunity level, they could ultimately influence component communities and parasite faunas (Poulin & Morand, 2004). At the component community level, Gutiérrez et al. (2017) found no association between helminth species richness and migration distance among populations of Charadriiform birds, suggesting that migration distance is not a universal predictor of parasite species richness in avian hosts. These inconsistent results may reflect fundamental differences among hosts groups, or simply differences in the hierarchical level of study. Moreover, bird community connectivity, rather than host species' dispersal potentials only, may promote the spread of parasites (Clark et al., 2018).

Furthermore, overall helminth richness increased with dietary breadth and tended to increase with habitat generalism (credible interval marginally crossing zero). Dietary breadth also showed a positive association with the richness of cestodes. Thus, as predicted, dietary breadth had a positive effect on tropically-transmitted helminths, in line with previous findings that bird species and populations exploiting diverse diets will encounter more parasite species during their lifetimes (Gutiérrez et al., 2017; Leung & Koprivnikar, 2016). These observations might have crucial consequences for host fitness, parasite biodiversity and conservation issues. Although the costs of immune defences trade-off against other components of host life-history (Norris & Evans, 2000), generalist host species exposed to

greater parasitic pressure might require greater immune investment than specialists (Gutiérrez et al., 2017; Leung & Koprivnikar, 2016). Indeed, variation in host defence strategies might influence the global distribution of hosts and their parasites as well as spillover risk to animal populations (Stephens et al., 2016); notably, bird species with stronger cell-mediated immune responses are more successful in becoming established (Møller & Cassey, 2004). Future comparative studies of parasite diversity and infection risk could be greatly advanced by combining indices of parasitic pressure and integrative measures of host immunocompetence (Buehler, Tieleman, & Piersma, 2010).

Additionally, although coloniality was not a strong predictor of overall parasite richness, colonial species tended to harbour more helminth species than non-colonial or semi-colonial ones. Indeed, cestode richness was lower in non-colonial host species than in colonial ones. Overall, this is consistent with the notion that group-living is likely to increase parasite transmission and ultimately richness (Rifkin, Nunn, & Garamszegi, 2012; Tella, 2002). Contrary to the general notion that host body size frequently shows a positive correlation with parasite species richness (Table 1), we did not find an association between host body mass and parasite richness at the level of total helminth richness. Surprisingly, within helminths, the richness of trematodes and acanthocephalans decreased with increasing host body size. As pointed by Kamiya et al. (2014), the independent effect of host body size on parasite richness can be obscured when comparisons are made across hosts with different trophic levels or living in different habitats; this may explain why this and other comparative studies did not detect a positive effect of host body size when phylogeny is taken into account (Cooper et al., 2012; Morand & Poulin, 1998; Nunn et al., 2003). Confirming that better studied species have more parasites than less well-studied species, citation count was positively correlated with parasite species richness, regardless of the parasite group considered. This highlights the need to correct for sampling effort in comparative studies of parasite diversity (Walther et al., 1995).



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Finally, although parasite diversity is considered to be a useful metric for estimating parasite pressures and impacts within and among hosts (Bordes & Morand, 2009; Morand, 2015), as well as for understanding the drivers of parasite transmission and infection risk (Johnson & Hoverman, 2012; Johnson, Preston, Hoverman, & Lafonte, 2013), it does not take into account potential variation in parasite abundance (i.e. prevalence within populations and intensity of infection within individuals). We therefore encourage future studies to develop and use more integrated indices of parasite diversity which incorporate parasite abundances (Bordes & Morand, 2009).

## 5 | CONCLUSIONS

In our analyses we found several correlates of parasite species richness in helminths (both for overall richness and separate groups) but none in haemosporidians infecting birds. Although we could not find strong statistical evidence for differences in the directionality of the effects between the groups, the approach of decomposing effects of host traits on major groups of macro- and microparasites is still useful for a deeper investigation of macroecological patterns of parasitism (Bordes & Morand, 2009). Furthermore, the lack of strong associations between haemosporidian species richness and host characteristics emphasizes the undiminished need to find the appropriate traits to model the distribution and diversity of vector-borne parasites with different environmental preferences if we are to anticipate disease emergence risks associated with global change.

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**DATA ACCESSIBILITY:** Data supporting the results are archived in Dryad Digital Repository: <http://doi.org/10.5061/dryad.sk5972v> (Gutiérrez et al 2019).

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## **SUPPORTING INFORMATION**

**Appendix S1.** Dataset.

**Appendix S2.** Supplementing the helminth database.

**Appendix S3.** Controlling for sampling effort.

**Appendix S4.** Colonial breeding.

**Appendix S5.** Phylogeny construction.

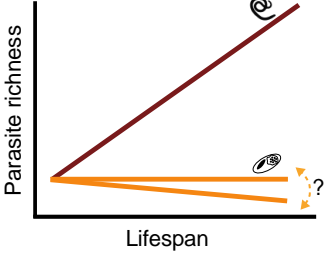

**Appendix S6.** Correlation matrices for predictor variables.

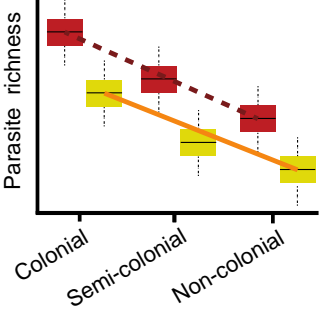
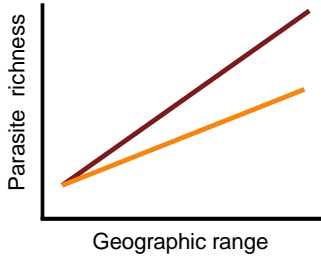
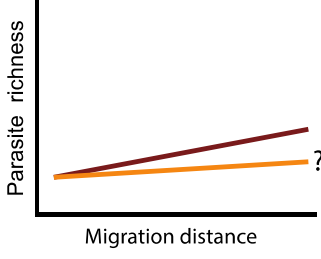
**Appendix S7.** Single- and multi-response analyses.

**Appendix S8.** Helminth group-specific analyses.

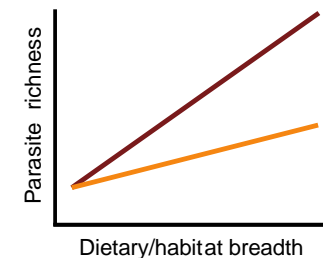
**Appendix S9.** Comparisons between migratory and non-migratory species.

**TABLE 1.** Hypotheses and predictions linking host traits to helminth and haemosporidian species richness. Predicted associations between helminth (dark red line) / haemosporidian richness (orange line) and host traits are presented as linear for simplicity.

Traits	General hypotheses	Predictions (for helminth/haemosporidian richness)	Visual predictions
Lifespan	Longer-lived host species might harbour greater parasite diversity since they might encounter more parasite species during their lifetimes (Poulin & Morand, 2004). Conversely, costs resulting from parasite exploitation might cause a negative association between parasite diversity and host longevity (Arriero & Møller, 2008; Cooper <i>et al.</i> , 2012).	Positive effect for less pathogenic and virulent helminths that seldom kill their host. Negative or no effect for more pathogenic haemosporidians, as number of parasite species has been associated with adult survival rate (Arriero & Møller, 2008).	
Body mass	Larger-bodied host species provide greater space and other resources to parasites and encounter them at higher rates (Poulin & Morand, 2004); they also have slower life histories and lower mortality rates, which might increase the ability of parasites to become established (Lindenfors <i>et al.</i> , 2007).	Positive effect regardless of the type of parasite considered. The effect is expected to be strongest for food-transmitted helminths as the higher intake rates of larger-bodied hosts would increase the probability of acquiring helminths.	

Coloniality	Parasitism is viewed as the primary cost of sociality. Group-living is often associated with significant costs due to the increased risk of parasite transmission, especially in colonial birds (Tella 2002; Rifkin <i>et al.</i> , 2012).	A positive effect of coloniality is expected, especially for environmentally transmitted parasites (fecal-oral transmission and from contaminated water, ground, or food) such as helminths.	
Geographic range size	Larger geographic ranges offer more opportunities for host-parasite associations to become established and encompass a greater diversity of habitats suitable for different parasites (Kamiya <i>et al.</i> , 2014; Clark <i>et al.</i> 2017).	Positive correlation; it should apply to all types of parasites but host range size should be more important for helminths, since they tend to be dispersal-limited (or not aided by a vector species), in contrast to haemosporidians.	
Migration	Migration may bring hosts in contact with “new” parasites thereby increasing parasite transmission in migratory birds (Koprivnikar & Leung, 2015; Leung & Koprivnikar, 2016). Conversely, migrations may lower parasite transmission by allowing hosts to escape parasites or by culling sick animals (Altizer <i>et al.</i> , 2011).	Migration tendency is expected to slightly positively correlate with parasite richness; the effect is expected to be more important for more dispersal-limited helminths.	

Dietary habitat breadths	Species with broader diet and habitat breadths are expected to harbour significantly more parasites than more specialized ones, as they might encounter more parasite species during their lifetimes (Gutiérrez et al., 2017; Leung & Koprivnikar, 2016).	As many helminths are food-transmitted parasites, dietary breadth is expected to be more positively associated with helminth than with haemosporidian richness. Habitat generalism should increase parasitism in both groups.
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## CAPTIONS TO FIGURES

**FIGURE 1.** The overlap in distribution of ranges (i.e. richness) of the bird species with (a) helminth data, (b) haemosporidian data, and (c) both helminth and haemosporidian data. Sample size for each subset is given between parentheses. Colder colours indicate lower species richness, while warmer colours represent higher richness. White areas are those where there are no species with data. Note that richness for (b) is almost identical to that for (c) because species composition is similar in both subsets.

**FIGURE 2.** Randomly sampled phylogenetic trees for bird species ( $n=327$  bird species belonging to 27 orders) with helminth richness data (a), and for bird species ( $n=145$  species belonging to 20 orders) with haemosporidian richness data (b). The evolution of parasite species richness is mapped on each tree using a colour gradient and the bars at the tips represent the values for overall richness. Bar plots showing the mean number of helminth parasites species (c) and haemosporidian parasites species (d) per host species (overall and relative to each parasite group; mean  $\pm$  SE). Silhouette illustrations came from PhyloPic (<<http://phylopic.org>>), contributed by various authors under Public domain license.

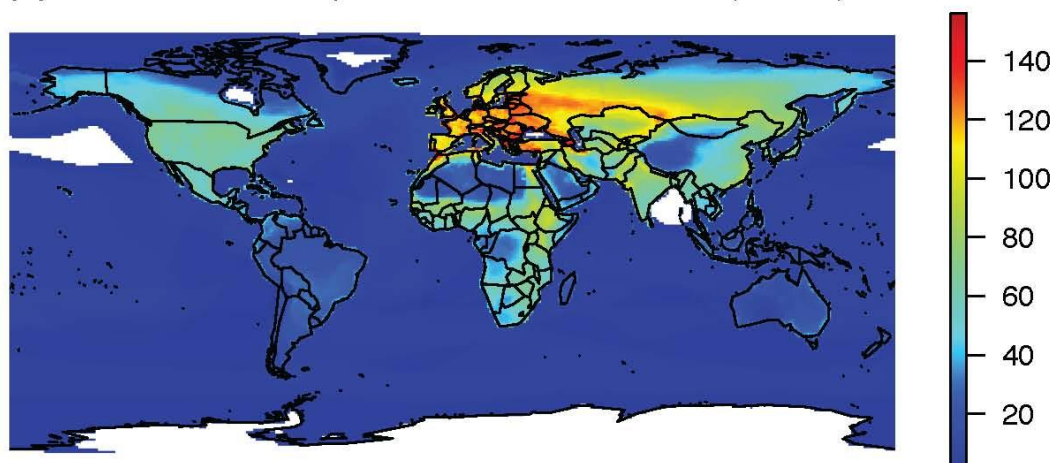
**FIGURE 3.** Effect of independent variables on helminth and haemosporidian richness across 327 and 145 bird host species, respectively. A summary of the important predictors for each parasite group is presented below. The posterior distribution of an independent variable with a negligible effect on parasite richness is expected to be centred on zero (dashed line); conversely, the distribution of an influential variable is expected to be substantially shifted from 0. Black dots indicate the mode of the posterior distribution and boxes indicate the 50, 75 and 95% credible intervals. Reference category for coloniality is 'colonial'.



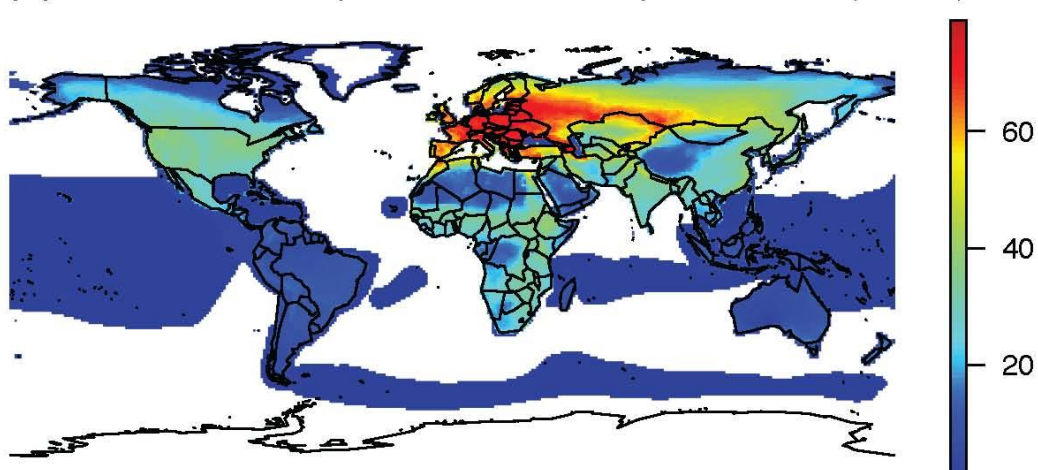
**FIGURE 4.** Mean heritability ( $h^2$ ) for helminth richness (red) and haemosporidian richness (orange) models. See *Methods* for details.

**FIGURE 5.** Effect of independent variables on the richness of different helminth groups across 327 bird host species. A summary of the important predictors for each helminth group is presented below. See Figure 3 for details.

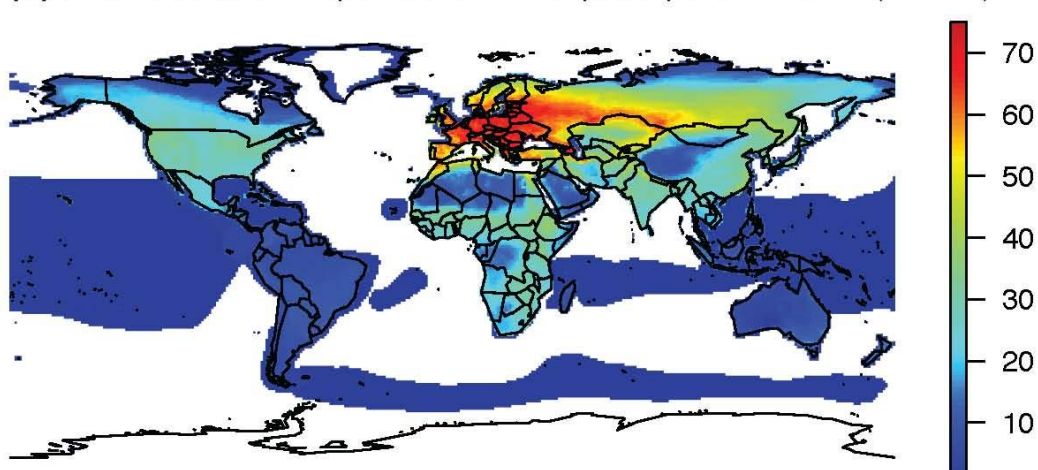
**(a)** Richness of bird species with helminth data ( $n=327$ )

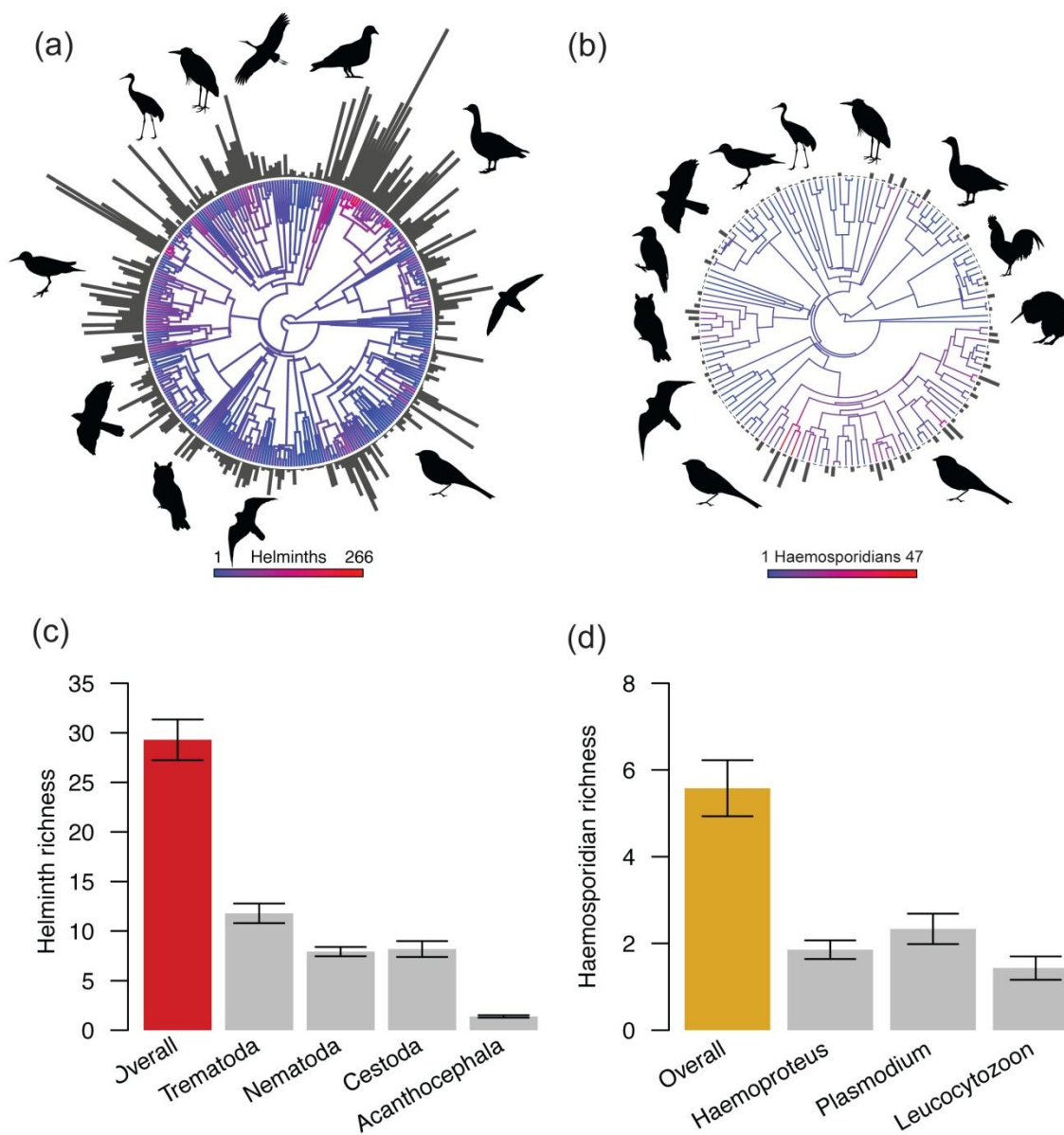


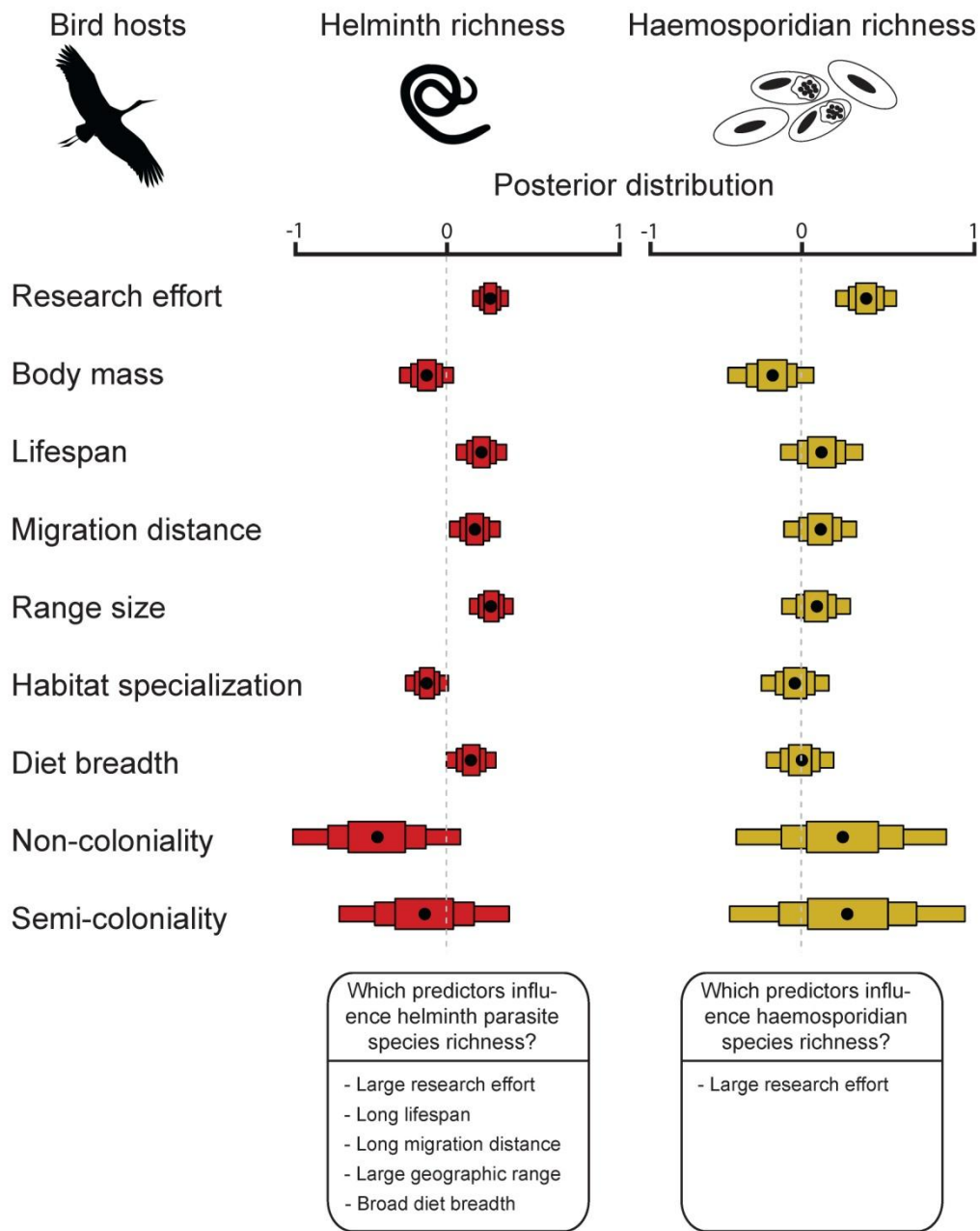
**(b)** Richness of bird species with haemosporidian data ( $n=145$ )

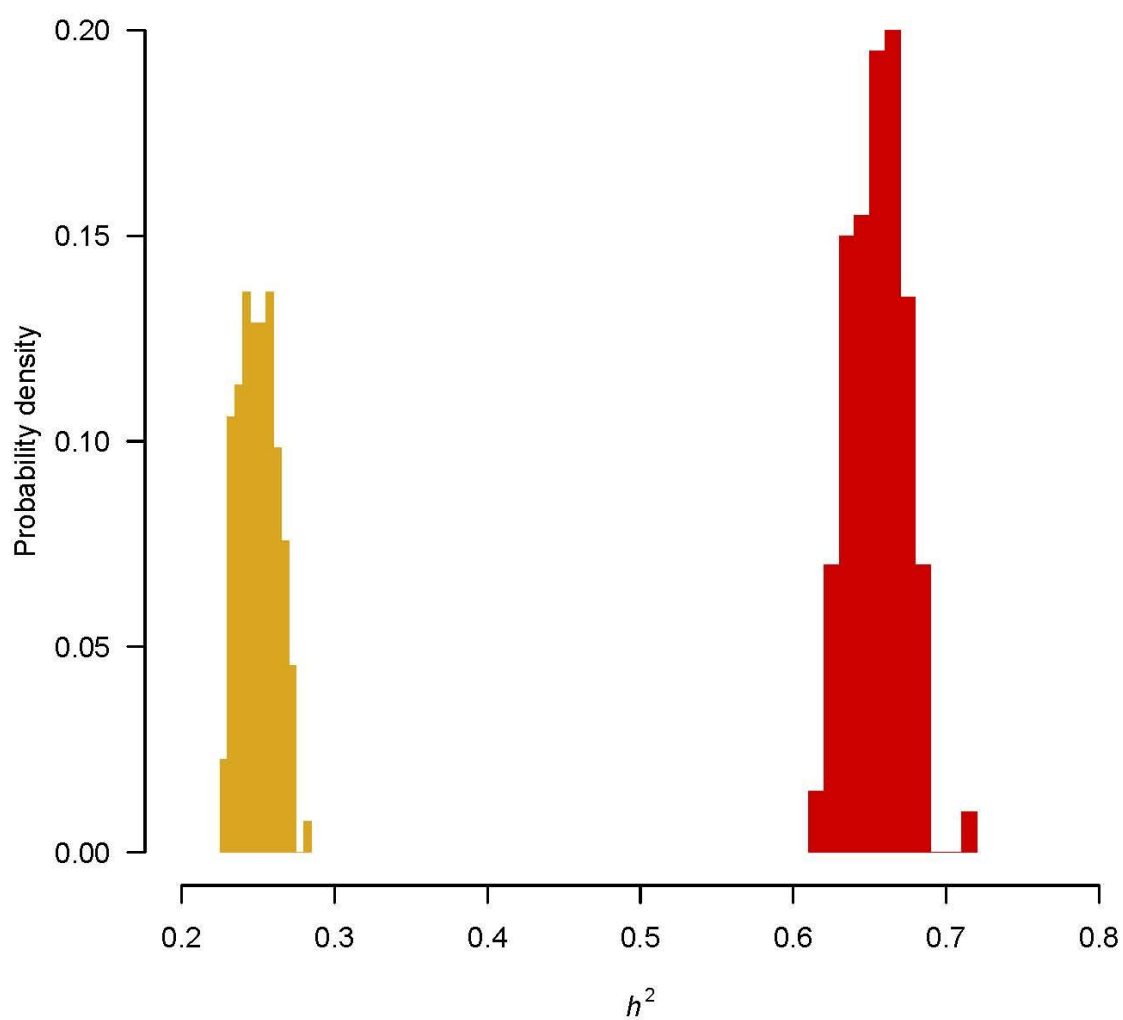


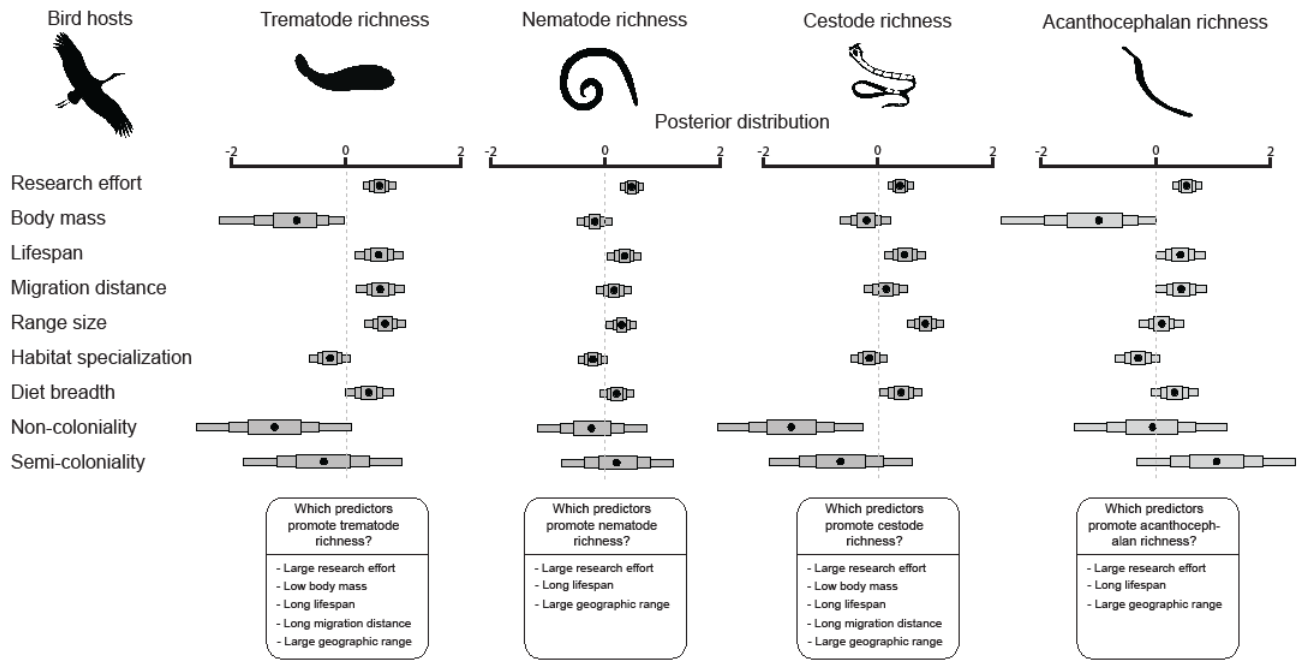
**(c)** Richness of bird species with complete parasite data ( $n=124$ )











I rematode richness